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DISTRIBUTION OF PHOSPHORUS IN GREAT POND, MASSACHUSETTS¹

By

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ABSTRACT

Inorganic phosphate and total phosphorus were determined during 1950 in Great Pond, Massachusetts. Except in deeper water during summer, the concentration of inorganic phosphate was less in Great Pond than in its sources of fresh and salt waters. In summer the total phosphorus concentration was greater in the Pond than in the Sound or River, this being particularly so in deep water of the Pond. During the remainder of the year concentrations were about the same in Sound, Pond, and River. Up to 92% of the total phosphorus within the Pond was organic phosphorus. The summer accumulation of phosphorus is explained as being the result of increased photosynthesis, the products of which settle from the surface to the deeper waters which return them up-pond in the countercurrent.

INTRODUCTION

Studies of the plankton ecology of coastal bays appear to show a greater productivity within these embayments than in the open ocean. For instance, Riley (1952) described a ten-fold increase in plant pigments in Long Island Sound when compared to the ocean beyond the eastern entrance. Tully (1949) showed greater oxygen saturation in the surface waters of Alberni Inlet than in the river feeding it or in the ocean at its mouth. Hutchinson and Lucas (1931) described much the same sort of situation at the mouth of the Fraser

¹ Contribution No. 748 from Woods Hole Oceanographic Institution.

River. In Oslo fjord, phytoplankton appeared to be greater in the inner reaches of the fjord (Braarud and Bursa, 1939). It would be of interest to know on what factors such enhanced productivity depends and how it is related to the hydrography, to the form of the basin, and to the land drainage.

Greater productivity within embayments could be the result of a locally enhanced rate of conversion of inorganic nutrients to organic substance without any increase in the quantity of nutrient elements present. Greater productivity could also result from contributions of nutrient substances by land drainage. Braarud and Bursa (1939) attribute the greater productivity in the surface waters of the inner portion of Oslo fjord to pollution from the city of Oslo. Finally, greater productivity could be produced by a suitable combination of hydrographic and biological factors such that the quantity of the nutrient element would be greater in the embayment than in the source waters, fresh and salt. Characterization of the organic content and of the processes that determine its production should lead to an understanding of features of phytoplankton growth that are indigenous and yet of general importance.

THE EMBAYMENT

Great Pond, a small estuary near Falmouth, Massachusetts, proved to be a convenient embayment in which to study features suggested by the foregoing considerations. Its hydrography has been well studied and reported by Barlow (1956). Fig. 1, which shows the shape and depth of Great Pond, reveals clearly its division into a wide portion, the main pond, and a narrow portion, the arm; it is 1.5 miles long, does not exceed 9 feet in depth at highest tide, and has a localized fresh and salt water inflow. Stations where samples were taken are numbered so that those with lower numbers are seaward, those with higher numbers landward.

METHODS

Measurements of inorganic phosphate and total phosphorus concentrations in the pond water were made along the axis of Great Pond at various times throughout 1950. At the same time phytoplankton cell counts and turbidity determinations were made. Water samples were taken from a rowboat within a space of several hours except during February and March, when they were taken from the shore. Water samples were obtained within several inches of the surface and approximately ten inches above the bottom.

Inorganic phosphate was determined by the Atkins-Deniges method,

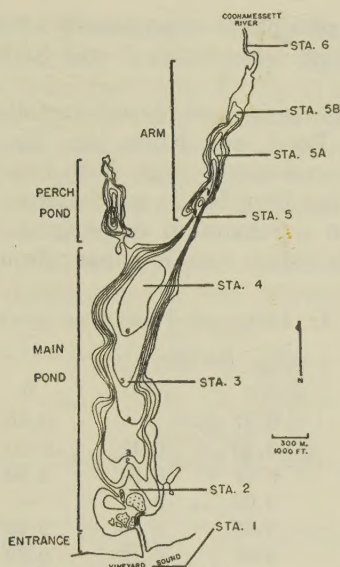


FIGURE 1. The morphometry of Great Pond. Depths are in feet.

total phosphorus by the Harvey method (1948). The difference between total phosphorus and inorganic phosphate was considered to be organic phosphorus. No attempt was made to separate the soluble and particulate fractions of organic phosphorus. The phytoplankton concentration was determined by counting all living cells under high magnification (X440) after filtration through a porcelain filter manufactured by the Selas Corporation. Turbidity determinations were the values of absorption of red light (0.66μ) in a four centimeter thickness of sampled water. Measurements of the fraction of light removed by representative samples were made with a photoelectric cell that was sensitive to all wave lengths of visible light. Thus, absorption values could be converted to extinction coefficients.

RESULTS

Distribution of Inorganic Phosphate. Table I gives an extract of the basic data. Table I and Fig. 2 show that the concentration of inorganic phosphate in surface waters was least in the midreaches of the Pond and that there was usually an increasing concentration of phosphate from midpond to the Sound and from midpond to the River. At times the gradient was relatively uniform but at other times it increased abruptly at the mouth of the River. In bottom

waters the inorganic phosphate concentration was variable; at times it was negligible and at other times it was higher than that in the Sound or River.

The changing concentrations of phosphate follow different seasonal cycles in the Sound, Pond, and River (see Fig. 3). In the Sound concentrations were consistently high from late summer to the end of winter; during spring they fell to a minimum in May, and during summer they rose to a maximum on August 23. In the surface waters of midpond the values were low throughout the year, February

TABLE I. INORGANIC PHOSPHATE, $\mu\text{g-at P/L}$

		Surface				Bottom	
Sts.		1	4	5a	6	4	5a
January	30	0.37	0.07	—	0.65	—	—
March	26	0.36	0.20	0.15	0.50	—	—
May	25	0.10	0.07	0.20	0.30	0.10	0.10
June	30	0.30	0.00	0.05	—	0.15	0.00
August	23	0.47	0.02	0.05	0.20	0.35	1.07
October	20	0.55	0.07	0.13	0.30	0.05	0.03
December	7	0.30	0.10	0.04	0.63	0.13	0.03

Total Phosphorus, $\mu\text{g-at P/L}$

Sts.		1	4	5a	6	4	5a
May	25	0.90	0.90	1.05	0.60	1.10	1.50
June	30	0.85	0.90	0.95	—	1.70	1.20
July	22	0.80	1.60	2.70	0.70	2.40	3.20
August	23	1.20	1.55	2.85	1.00	1.75	7.00
October	20	1.20	0.85	0.50	0.35	1.40	1.00
December	7	1.00	0.50	1.25	1.00	0.70	1.40
January	10	1.00	0.60	0.40	0.70	0.50	0.80

25, March 6, and July 22 being the only exceptions. Comparison of the concentrations at Sts. 1 and 4 shows large gradients in fall and winter and slight gradients in late spring and early summer (see Fig. 7). In the River, concentrations were higher in winter and lower in summer. The seasonal cycles at Sts. 1 and 6 were roughly similar except that the maximum and minimum of the River were later by two to four months than those of the Sound. Inorganic phosphate in the bottom water of the Pond, represented by Sts. 4 and 5a, was low in the fall, at the end of May, and during June, resembling the surface concentrations. During July and August it rose to high values. At St. 4, values were higher in July than in August, while farther up-pond at St. 5a the reverse was observed.

Distribution of Total Phosphorus. In summer, total phosphorus concentrations were usually considerably higher within the Pond than in the Sound or River (see Table I, Fig. 4) and were much greater in the bottom water of the Pond than at its surface. Thus, the chief total phosphorus gradients were negative from Pond toward Sound or River. During the remainder of the year, total phosphorus within the Pond was approximately the same as or slightly lower than that in the Sound or River.

The seasonal cycle is shown in Fig. 5. In the Sound a slight increase in total phosphorus during summer was followed by a decrease there-

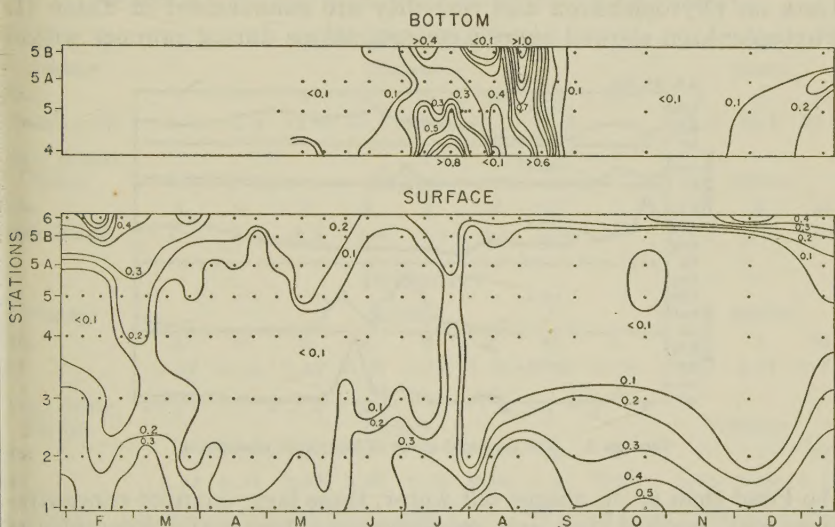


FIGURE 2. The distribution of inorganic phosphate in time and space. Concentrations are expressed in $\mu\text{g-at P/L}$.

after. The surface waters of midpond had about the same cycle as the Sound. On several dates during summer, values in midpond were slightly higher than those in the Sound or River, and during the latter part of the year, values were slightly lower than those in the Sound or River. In the River there was little seasonal change.

Bottom samples contrasted sharply with surface samples in that total phosphorus increased to much higher concentrations during summer. Both Figs. 4 and 5 show these conditions. It is clear that the increases were larger and later at up-pond St. 5a than at mid-pond St. 4.

In the Sound, 71% of the total phosphorus was organic, on the annual average; at the surface in the arm, 91.5% was organic phos-

phorus. These values spanned values at other locations. Therefore, the distribution of organic phosphorus was similar to that of total phosphorus, with the exception that throughout summer there was a distinct negative gradient in the surface water from the arm to the Sound. As for total phosphorus, the concentrations in the bottom water increased during summer to much higher values at up-pond St. 5a than at midpond St. 4 (see Fig. 5). At St. 5a this increase occurred later in the summer than the lesser increase at St. 4.

Relation of Organic Phosphorus to Phytoplankton and Turbidity. Data on phytoplankton and turbidity are summarized in Table II. Phytoplankton showed greater concentrations during summer within

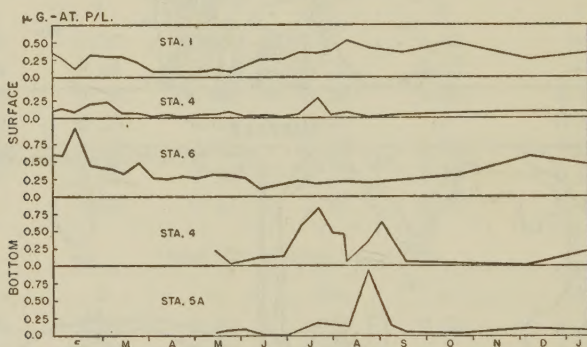


FIGURE 3. The seasonal cycle of inorganic phosphate.

the Pond than in the source salt water; these large summer concentrations were greater than any concentrations during the remainder of the year. A similar situation existed for turbidity, amounts within the Pond in summer being greater than those of the source salt and fresh waters and exceeding values anywhere at other seasons. Surface and bottom concentrations of phytoplankton were approximately the same; much greater turbidity was present in deep water than at the surface, particularly in summer. Fig. 6 shows the relation of phytoplankton and turbidity at two bottom stations. During summer, phytoplankton increases were roughly paralleled by increases in turbidity; this is particularly well shown by the correlation of the monthly means of phytoplankton concentration and turbidity. It is noteworthy that at up-pond St. 5a a greater amount of turbidity is associated with phytoplankton concentration than at St. 5. The changes in phytoplankton concentration throughout summer were erratic, whereas turbidity showed somewhat smoother changes

Thus, in water of the same turbidity the quantity of phytoplankton was low on one date but high on another. These features suggest that the large concentrations of organic phosphorus in summer could be attributed, in part, to the large concentrations of phytoplankton and particulate matter that cause turbidity. Since turbidity and phytoplankton were related in a general way by monthly averages, this particulate matter would appear to be derived from phytoplankton. Since, however, the ratio of turbidity to plankton fluctuat-

TABLE II. SEASONAL AVERAGES OF PHYTOPLANKTON AND TURBIDITY

PHYTOPLANKTON											
Summer			Surface						Bottom		
Sts.	1	2	3	4	5	5a	5b	6	4	5	5a
Cells/1 x 10 ⁶	1.8	5.9	13.6	17.8	25.5	22.9	22.4	—	16.4	26.0	20.9
Fall, Winter, Spring											
			Surface						Bottom		
Sts.	1	2	3	4	5	5a	5b	6	4	5	5a
Cells/1 x 10 ⁶	5.7	8.3	7.9	6.5	8.4	9.0	4.0	—	7.1	11.3	12.0
TURBIDITY											
Summer			Surface						Bottom		
Sts.	1	2	3	4	5	5a	5b	6	4	5	5a
k*	0.37	0.44	0.55	0.95	1.15	1.09	1.32	0.69	1.68	2.17	2.51
Fall, Winter, Spring											
			Surface						Bottom		
Sts.	1	2	3	4	5	5a	5b	6	4	5	5a
k*	1.91	0.72	0.53	0.67	0.76	0.93	0.67	0.63	1.04	0.90	1.13

* k is the extinction coefficient in the equation, $I_z = I_0 e^{-kz}$, where I_0 and I_z are respectively light intensities at the sea surface and at depth z (in meters).

ed greatly from time to time, the turbidity did not appear to be related directly to plankton numbers. One is led to believe that the accumulated remnants of dead phytoplankton cells persisted, thus causing turbidity in the pond water and accentuating its organic content.

It is possible that, during summer, turbidity was accentuated by silt from river water or by stirring of bottom mud. However, this possibility appears to be minimal, since the river water (St. 6) was relatively clear and since winds and tidal action were less in summer than in fall or winter.

THE EFFECT OF UPWELLING ON THE PHOSPHORUS DISTRIBUTIONS

During summer the surface water of the arm usually had a salinity of less than 15‰ while the bottom water there had a salinity greater than 25 ‰. However, on July 22 the surface waters of the arm had salinities in the neighborhood of 25 ‰ as a result of a north wind blowing surface water downpond with consequent upwelling of deep water to the surface. Both inorganic and total phosphorus concentrations in the surface of the arm were much higher on this day

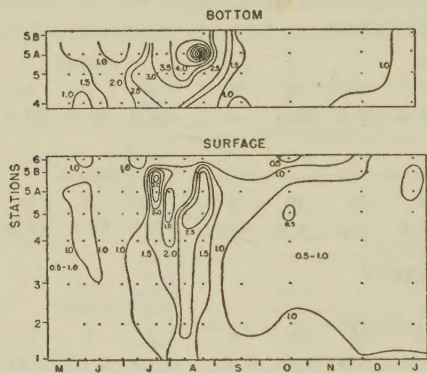


FIGURE 4. The distribution of total phosphorus in time and space. Concentrations are expressed in $\mu\text{g-at P/L}$.

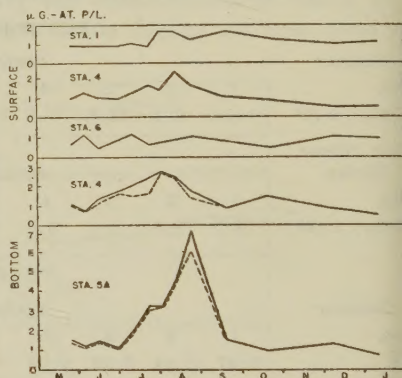


FIGURE 5. The seasonal cycle of total phosphorus (solid line) and organic phosphorus (dashed line).

than on previous days in the summer and they were rather similar to the concentrations in the bottom water (see Figs. 2 and 4).

When bottom concentrations of total phosphorus were the same as those in the main pond or River, upwelling caused no discernible change in the pattern of distribution, as can be seen by comparing data of December 7, a day of upwelling, with data of May 25, a normal day. When bottom concentrations of inorganic phosphate were negligible (fall and winter), the data for days of upwelling (September 18, October 20) showed that there were negligible concentration at all surface stations in the arm, an abrupt increase occurring at the mouth of the River. Normal days, such as May 25, showed usually intermediate values between those in the River and those at midpond.

CHARACTERISTICS OF THE PHOSPHORUS GRADIENTS

In general, the concentration of inorganic phosphate decreases from the Sound and from the River toward the midreaches of the Pond. At the surface the gradient is always present (see Fig. 7). Only between waters of the Sound and the bottom water of the Pond

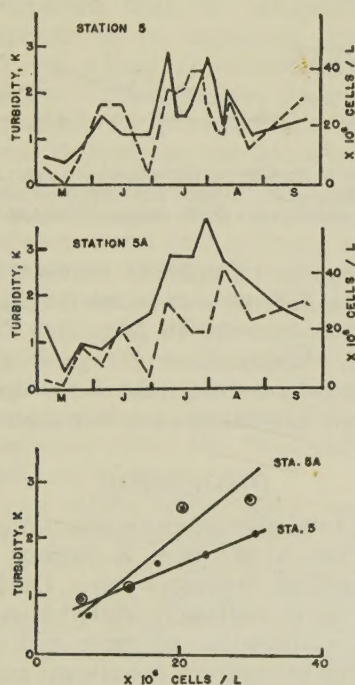


FIGURE 6. The relation of phytoplankton and turbidity in the bottom water. In the upper two graphs the dashed line represents phytoplankton and the solid line turbidity. In the lower graph unencircled points are monthly means for May through August at St. 5; encircled points are those at St. 5a. Turbidity is expressed as the extinction coefficient, k (see Table II).

or between water of the River and the bottom water of the Pond, during July and August, is this gradient reversed. When the difference between the water of the Sound and the average of surface and bottom water in midpond is plotted for the year, as in Fig. 7, this inward gradient is almost always present. This indicates that inorganic phosphate is being consumed in the synthesis of organic matter to a greater extent within the Pond than in the Sound or River. It also indicates that tidal mixing along the Pond is perpetually transporting inorganic phosphate into the Pond.

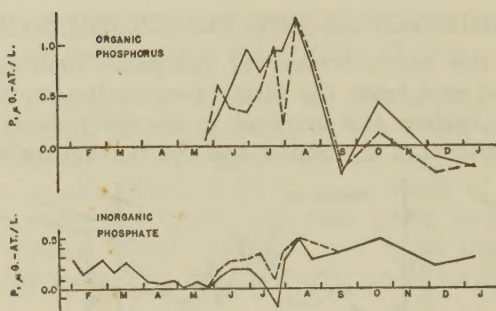


FIGURE 7. The difference in phosphorus throughout the year; upper graph, St. 4 minus St. 1; lower graph, St. 1 minus St. 4. Dashed lines represent the use of the surface value at St. 4 and solid lines represent the use of the average of surface and bottom at St. 4.

The gradient in organic phosphorus between the Pond and the Sound is shown as the difference between its concentrations at Sts. 4 and 1 from May 25 to January 10 (Fig. 7). The gradient is large during summer only. Elaboration of organic phosphorus appears to occur to a greater extent within the Pond than in the Sound or River, where the mean amount is even less than that in the Sound.

DISCUSSION

At the end of May, total phosphorus is essentially uniform. During summer it increases two to six times in various parts of the Pond, this increase being greatest in deep water. During fall and winter total phosphorus is again uniformly distributed. The gradient of inorganic phosphate is inward at all times and upward in summer. The gradient of organic phosphorus is outward and upward.

The accumulation of organic phosphorus in summer may be explained in the following manner. Inorganic phosphate is transported inward from the Sound and from the River by tidal mixing; evidence for this is found in the gradient. Inorganic phosphate is converted to organic phosphorus by photosynthesis, the high phytoplankton concentration within the Pond being indicative of photosynthetic conversion. Organic phosphorus accumulates in the bottom water due to the sinking of photosynthetic products, evidence for which is found in the vertical stratification of turbidity but not of phytoplankton. Organic phosphorus is transported seaward due to its gradient. Thus, losses of organic phosphorus from surface waters are in two directions, outward and downward. As indicated by the salinity distribution (Barlow, 1956), the deep water has a net drift upstream and carries with it the organic phosphorus lost from the

surface by sinking. This feature accounts for the fact that the greatest accumulation is found at St. 5a, well up the arm, and explains why the turbidity-phytoplankton ratio is greater at St. 5a than at St. 5. Surface accumulation of organic phosphorus at Sts. 4 and 5 is due to renewal of surface water by deep water through mixing and upwelling. It is apparent that the accumulation of phosphorus during summer depends on an enhanced photosynthetic activity whereas during fall and winter photosynthesis is lessened and the accumulated phosphorus is removed from the pond water.

Unsolved is the problem as to what extent summer accumulation of organic phosphorus depends on the hypothetical mechanism just described, which involves simple hydrography primarily, and to what extent it depends on exchanges with the bottom sediment. Phosphorus exchange between water and sediment has been well demonstrated in a lake (Mortimer, 1941) and in an estuary (Miller, 1952). Part of the summer accumulation may become entrapped in the bottom mud, to be released again the following summer. During fall and winter organic phosphorus may settle to the bottom, to remain until the enhanced regenerative processes of summer release it again. Evidence for the latter process is found in the slightly lower surface values of total phosphorus within the Pond than in the source fresh and salt waters in fall and winter.

Greater productivity within embayments than in the ocean may result in three ways: by enhanced conversion of inorganic nutrients, by contributions of nutrients from land drainage, and by accumulation of nutrients. It is concluded that the exceptional productivity of Great Pond is an example of the third way, wherein a combination of hydrographic and biological factors cause the nutrients to accumulate in greater concentrations than are present in the sources of fresh and salt water.

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EFFECT OF WIND ON SALINITY DISTRIBUTION IN AN ESTUARY¹

By

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ABSTRACT

The distribution of salinity in a small tidal estuary, Great Pond, through a period of over a year is described. The numerous important variations in salinity, both seasonal and short-term, cannot be attributed to tides or to day-to-day changes in the supply of fresh water. It is shown that they are related to day-to-day changes in wind force and direction and that the general seasonal change in average salinity is related to a general seasonal change in prevailing winds.

INTRODUCTION

Of the important time and space variations in properties of estuaries, the most striking are those of salinity. Salinity variations are of particular significance since they may represent marked changes in both the accumulation and distribution of fresh and salt water. Some variations in salinity can clearly be attributed to climatic and seasonal changes in the fresh water supply from land drainage; others are of such short duration and irregular occurrence that their causes are not immediately apparent.

These salinity variations appear to be especially marked in the smaller and shallower estuaries, such as those dissecting the southern shore of Cape Cod. Ketchum (1951) has discussed the circulation and tidal exchanges in one of these small estuaries, Great Pond, near Woods Hole, Massachusetts, and the purpose of this paper is to present the results of a year's study of the variations in salinity of this same estuary. The salinity data have been collected during seasonal surveys of biological and chemical properties of this pond (Barlow, 1955; Hulburt, 1956) and during several detailed hydrographic studies. These data give an exceptionally detailed description of the salinity variations in this estuary and provide the basis for an understanding of their causes.

¹ Contribution No. 752 from the Woods Hole Oceanographic Institution.

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METHODS AND SOURCES OF DATA

Great Pond (Fig. 1) is the drowned mouth of a small river, the Coonamessett, which now provides the principal source of fresh water for the pond. Great Pond's northern portion, the arm, is shallow and muddy and is surrounded by high banks and trees which shelter it from most winds. The narrows and main pond are deeper, sandier, and more exposed to winds from all directions. The extensive shallows in the southern end were apparently formed by sand drifting into the pond from Vineyard Sound. The narrow entrance from Vineyard Sound is maintained in the barrier beach by a set of stone revetments and jetties.

Twenty-eight regular surveys of the plankton, salinity, phosphate, and temperature were made between March 20, 1950 and July 7, 1951. Surface and bottom salinity samples were usually taken at

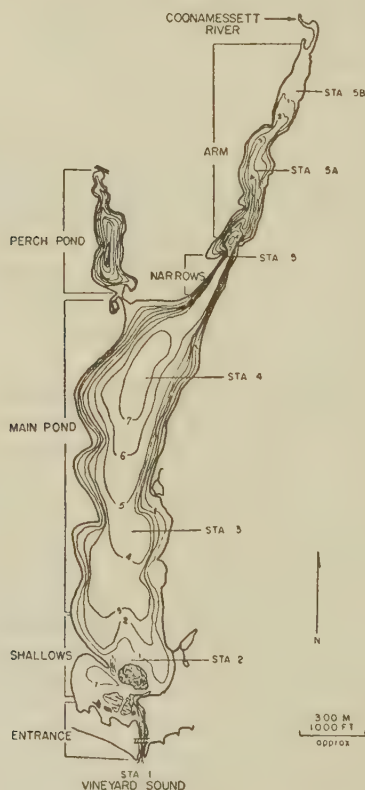


Figure 1. Chart of Great Pond. Depths in feet

all of the stations shown in Fig. 1. During spring and summer of 1950, observations were taken at about 10 to 15 day intervals, but during the following winter and spring they were less frequent and less detailed. Intensive surveys during which the salinity distribution was studied in greater detail throughout several stages of the tide were made on June 3 and 26 and August 29, 1950.

Rainfall measurements near the pond were provided by Mr. Wilfred Wheeler of Falmouth, Mass. Wind velocity and direction were recorded on each sampling day; wind measurements recorded at Nantucket Lightship and published by the U. S. Weather Bureau have also been used. River flow just north of Great Pond was measured at irregular intervals.

THE SALINITY DISTRIBUTION AND ITS VARIATIONS

A number of samples taken across the pond have shown only small east-west salinity differences, seldom exceeding 3‰. However, since the river water tends to flow over the mixture which it forms with Vineyard Sound water, there may be large differences at the surface and bottom in parts of the pond. Discussion of the salinity will therefore be limited to the vertical distribution along the land-sea axis of the pond.

Several typical salinity distributions are shown in Fig. 2. The distribution observed on August 29, 1950 is of special interest because the meteorological conditions were then so typical of the most frequent conditions during summer. Vertical and horizontal gradients were strongest in the arm and narrows. In the arm, the surface salinity ranged from zero at the river mouth to over 20‰ at the narrows and was from 10 to 15‰ less than the salinity of the bottom water. The gradients were much less in the main pond.

There were many temporary variations. Sometimes, when the pond was everywhere nearly isohaline from surface to bottom, the salinity gradients were horizontal and were strongest between the pond and the arm, as on June 3. At other times, as on June 26, there were only small and irregular horizontal salinity differences; at such times the gradients were predominantly vertical.

The seasonal distribution at the surface is shown in Fig. 3. It is seen that there were large and abrupt changes in the extent and freshness of the brackish surface layer, which was most pronounced in summer when it usually extended far down the arm into the main pond. In winter, however, the brackish layer seldom extended far from the river. The mean surface salinities in the arm and northern end of the main pond were therefore higher in winter than in summer,

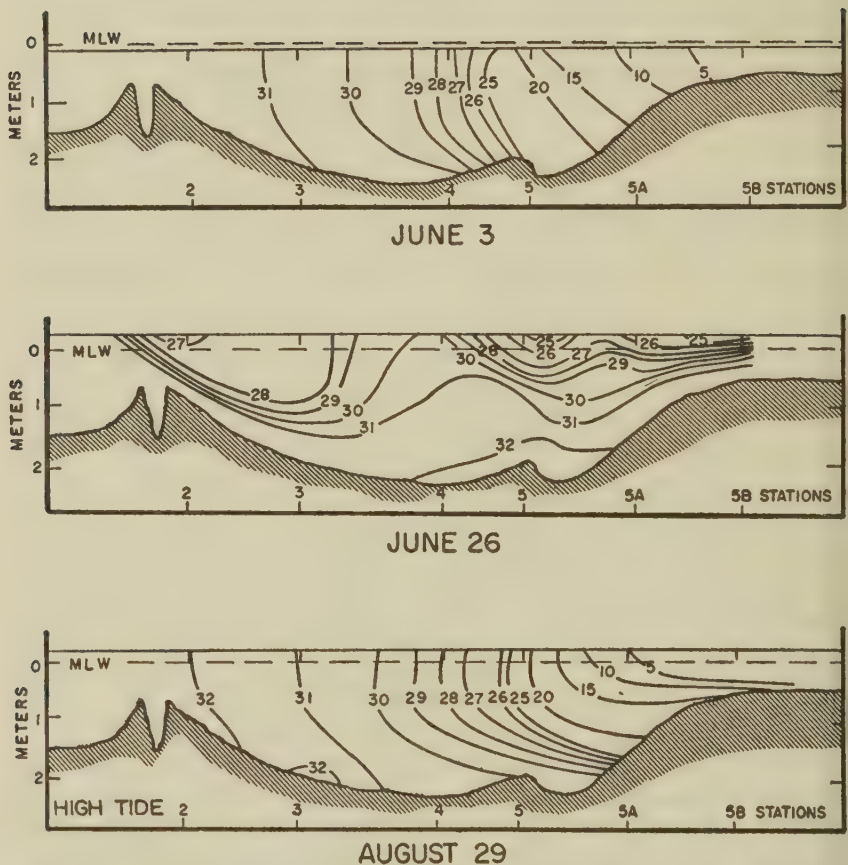


Figure 2. Vertical distribution of salinity (‰) on June 3, June 26, and August 29 at high tide. Station 1 at left of diagram. Broken line represents mean low water.

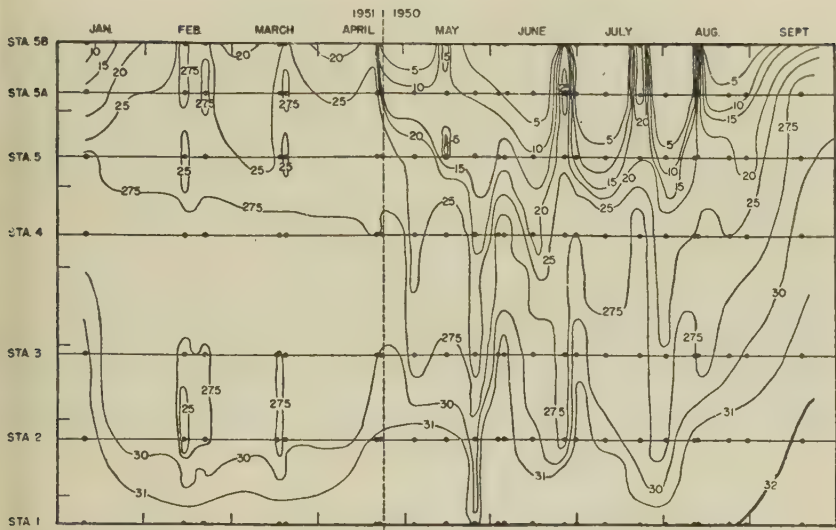


Figure 3. Seasonal distribution of surface salinity (‰). Closed circles indicate observations.

as shown in Table I. The deeper water in most of the arm and main pond and the surface water in the southern part of the main pond had but small variations seasonally or within seasons.

TABLE I. MEAN SALINITIES (‰) AND THEIR RANGES IN GREAT POND

Summer: May 4–August 23, 1950

Winter: Sept. 18, 1950–Apr. 22, 1951

Station	Summer			Winter		
	Mean	Min.	Max.	Mean	Min.	Max.
1, surface	31.68	31.48	32.09	31.73	31.29	32.32
2, surface	30.56	27.30	31.89	29.11	26.11	32.23
3, surface	27.84	23.08	31.36	29.23	27.18	31.30
4, surface	24.49	14.45	28.83	29.61	27.66	30.01
bottom	30.87	27.99	32.09	30.58	29.22	31.31
5, surface	14.42	3.59	24.47	25.09	11.08	29.85
bottom	29.82	25.99	31.51	29.59	26.87	31.11
5a, surface	10.02	2.35	28.00	25.43	16.00	30.62
bottom	27.92	21.44	30.97	29.02	25.02	30.84
5b, surface	7.21	0.02	25.49	17.60	0.39	29.36
bottom	23.92	1.51	30.77	23.87	3.23	30.37

CAUSES OF VARIATIONS IN SALINITY

Effect of Tides. During the three intensive surveys, horizontal displacement of the salinity was observed at various stages of the tide. These observations showed that some of the differences from survey to survey in the southern part of the pond are probably related to the state of the tide when the surveys were made. However, horizontal movements cannot account for the large changes in the rest of the pond between some of the surveys.

Effect of Variations in the Supply of Fresh Water. During most of the year variations in river flow are caused by variations in precipitation, which in this region changes but little from season to season on an average monthly basis (Table II). Although the river flow

TABLE II. TOTAL MONTHLY RAINFALL (INCHES) AT FALMOUTH, MASSACHUSETTS, 1950 AND 1951*

	1950	1951
January	3.15	3.39
February	4.39	3.26
March	4.47	4.16
April	3.98	2.54
May	2.67	3.96
June	3.83	1.35
July	1.90	1.47
August	4.13	5.43
September	3.24	1.24
October	1.04	2.95
November	6.25	4.20
December	3.08	4.87

* Recorded by Mr. Wilfred Wheeler, Falmouth, Mass.

may change as much as five-fold in two days when large volumes of water stored in reservoirs are released into the valley in spring and fall for the benefit of local cranberry culture, none of the salinity surveys was made when the river flow was so markedly changed. On the basis of our observations seasonal differences in the salinity distribution are evidently not caused by seasonal changes in the supply of fresh water. In fact, in winter and spring, when surface salinities in the pond are highest, precipitation is greater than the yearly average, and in summer, when surface salinities are lowest, the rainfall is lower than average.

Heavy rainstorms, however, may cause immediate but temporary increases of from two to six times in the river flow, and since the surface of the arm is likely to be effected most by these increases, and

attempt was made to relate changes in its salinity to changes in rainfall. It appears that salinity of the arm is not effected by rainfall on the day of sampling or by total rainfall during the two, five, or ten days preceding the day of sampling.

Although many of the salinity changes are doubtless caused by changes in total amounts of fresh water in the pond, only the intensive surveys of June 26 and August 29 were detailed enough for satisfactory estimates. Despite a smaller flow in the river on August 29, the fresh water in the pond was twice the amount found on June 26 (see Table III). This increase in fresh water was accompanied by such a decrease in river flow that the flushing time (Ketchum, *et al.*, 1951) on August 29 was more than five times that on June 26. These results differ sharply from those of circulation studies in other estuaries, such as Alberni Inlet (Tully, 1949) and the New York Bight (Ketchum, *et al.*, 1951), where it has been shown that increases in river flow tend to be accompanied by such increases in the accumula-

TABLE III. RIVER FLOW AND FRESH WATER IN GREAT POND

	<i>River flow per hour</i>	<i>Total fresh water</i>	<i>Flushing time</i>
June 26, 1950	$1.8 \times 10^3 M^3$	$114 \times 10^3 M^3$	2.66 days
August 29, 1950	$0.75 \times 10^3 M^3$	$230 \times 10^3 M^3$	12.7 days

tion of fresh water that the flushing time remains relatively little changed.

Effect of Variations in Wind. In Great Pond, variations in wind force and direction are the principal cause of variations in the distribution of fresh and salt water, both vertically and horizontally.

When the wind force is 0, the river water flows seaward in a shallow surface layer that is only gradually mixed with salt water. When this condition obtained on May 25 there was a shallow brackish layer extending far down the pond (Fig. 3); only in the shallows and at the southern entrance to the pond was tidal turbulence adequate to produce mixing from surface to bottom. On the other hand, strong winds may increase the vertical mixing so much so that the salinity in the pond is everywhere nearly homogeneous from top to bottom, as on June 3, when the wind was southeast and its force 4.

Though the wind plays an important part in vertical mixing, it has its most marked and probably its most important effect on horizontal distribution, particularly in the arm.

We have examined the relation between the salinity and the wind component parallel to the long axis of the pond, the latter being

computed from the mean wind force and direction observed at Nantucket Lightship in the 24 hours preceding sampling. Wind directions at Nantucket Lightship were nearly the same as those at the pond at the time salinities were measured.

In Fig. 4a it is seen that, in the arm, winds directed seaward along its axis are associated with high surface salinities, while winds directed landward are associated with low surface salinities. Hence changes in wind direction are accompanied by abrupt changes in the salinity

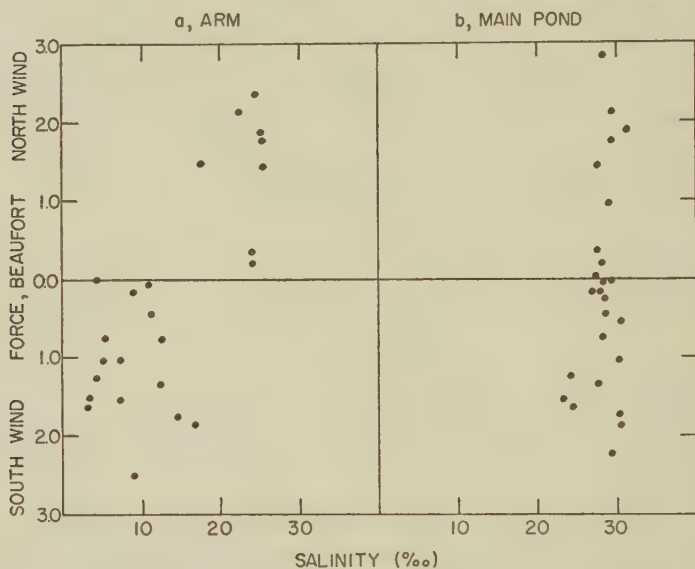


Figure 4. Wind force and direction relative to salinity of the arm and of the main pond. Wind force is north or south component of average Beaufort wind force reported at Nantucket Lightship in 24 hours preceding sampling. Salinities are mean surface salinities.

of the arm. For example, a shift in wind from south on August 11 to north on August 12 caused rapid increases in surface salinity; on August 11 the wind had a component of 0.8 from the south and on August 12, 2.4 from the north (Fig. 3). Inversely, when the wind changed from north on April 21 to south on April 22 there was a rapid decrease in surface salinity; on April 21 the wind had a component of 1.8 from the north and on April 22, 1.8 from the south (Fig. 3).

In the main pond, however, winds seem to have much less effect on the salinity than in the arm (Fig. 4b), probably due in large measure to differences in the topography of the land around the arm and the

pond. While the arm is effectively shielded from all winds but those directly landward or seaward, the main pond is exposed about equally to winds from all directions. Nevertheless, on the three occasions when the mean surface salinity in the main pond was below 25‰ there were strong southerly winds.

During the intensive surveys of June 26 and August 29 both current and salinity at the entrance were measured at half-hourly intervals. From these data, volumes of flow and exchanges of fresh water were estimated (see Table IV). Unfortunately the observations did not

TABLE IV. EXCHANGE OF WATER BETWEEN GREAT POND AND VINEYARD SOUND AS AFFECTED BY WIND DIRECTION

Date	June 26	August 29
Wind direction	Northerly	Southwesterly
Period of Ebb (southerly)	0950-1430 4.7 hours	1148-1300; 1430-1900 5.9 hours
Period of Flood (northerly)	1430-1900 4.5 hours	0745-1148; 1300-1430 5.5 hours
Total Flow, Ebb	$438 \times 10^3 \text{M}^3$	$470 \times 10^3 \text{M}^3$
Total Flow, Flood	$756 \times 10^3 \text{M}^3$	$411 \times 10^3 \text{M}^3$
Net Loss	$-318 \times 10^3 \text{M}^3$	$59 \times 10^3 \text{M}^3$
Fresh Water Loss, Ebb	$59 \times 10^3 \text{M}^3$	$2.91 \times 10^3 \text{M}^3$
Fresh Water Gain, Flood	$15 \times 10^3 \text{M}^3$	$1.14 \times 10^3 \text{M}^3$
Net Loss	$44 \times 10^3 \text{M}^3$	$1.77 \times 10^3 \text{M}^3$
Net Loss per Hour	$4.8 \times 10^3 \text{M}^3$	$0.15 \times 10^3 \text{M}^3$
River Flow per Hour	$1.8 \times 10^3 \text{M}^3$	$0.75 \times 10^3 \text{M}^3$
Fresh Water Content of Pond	$114 \times 10^3 \text{M}^3$	$230 \times 10^3 \text{M}^3$

include a complete tidal cycle, but the periods of ebb and flood observed were about equal. With northerly winds of force 3 and with the flood into the pond greatly exceeding the ebb, the fresh water content of the pond was relatively low; $44 \times 10^3 \text{m}^3$ of fresh water escaped from the pond. With southwesterly winds of force 2 only $1.77 \times 10^3 \text{m}^3$ of fresh water escaped. Thus, with northerly winds the net loss of fresh water per hour of observation was three times greater than the rate of river flow whereas with southwesterly winds the loss was only 1/5 the river flow. Obviously, then, northerly winds facilitate the loss of fresh water from the pond while southerly winds retard it.

Seasonal changes in salinity distribution have been summarized in Table I, which shows that all of the average surface salinities in the arm in summer were 10 to 15‰ lower than surface salinities in

winter. In the main pond, however, there appear to be no significant seasonal changes in surface salinity.

As would be expected from the foregoing discussion, these seasonal changes in salinity in the arm are also associated with changes in wind direction and force. The northerly or northwesterly winds that prevail in fall, winter and spring allow relatively little fresh water to accumulate in the arm; obviously this results in higher salinities there in winter. Of the seven winter surveys (January through April 1951) which were detailed enough to show the salinity of the entire pond, only two (January 10, April 22) were made on days when the wind had components from the south, and it was only on those days that surface salinities were as low as those which are usual during summer when southwesterly winds prevail.

From May through August in 1950 and 1951 the wind had components from the south on 15 of the 18 days it was observed at the pond. These southerly winds allowed more fresh water to accumulate in the arm, hence surface salinities were generally lower than those found in winter. On the remaining three of those 18 days (June 26, July 22, and August 12, 1950) the wind had components from the north, and on those days the surface salinities in the arm were as high as usual during the winter.

ACKNOWLEDGEMENTS

These studies were suggested by Dr. Alfred C. Redfield, to whom the author is indebted for his continued encouragement and advice. The author has also benefited from discussion of this problem with Dr. Bostwick H. Ketchum.

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ON THE RANGE OF VARIATION IN SEA LEVEL

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ABSTRACT

It is inferred from statistical theory that under 'stationary' conditions, *i. e.*, in the course of periods during which the mean sea level remains stable, the average range of sea level for intervals of time of given lengths should vary linearly with the logarithm of the length of time interval. This is an asymptotic property, so that the logarithmic law of increase in range holds only if the intervals considered are relatively long.

To check on the inference, data of sea level at Tel Aviv are studied. It is confirmed that the average monthly, two-monthly, . . . , yearly, . . . ranges closely follow a logarithmic law of increase.

1. STATISTICAL THEORY

1.1 Let x be a continuous variable with a probability distribution, $f(x)$ the frequency function of the distribution, and $x_1, x_2, \dots, x_k, \dots, x_n$ independent samplings of the variable taken successively. The range is the greatest member of the set of differences $|x_k - x_{k+l}|$, $k = 1, 2, \dots, n-1$, $l = 1, 2, \dots, n-1$, $k+l \leq n$. To find the range as a function of sample size n , we shall first have to consider the distribution of the differences $|x_k - x_{k+l}|$.

Let us denote the difference $|x_k - x_{k+l}| = |x_{k+l} - x_k|$ by r , $r \geq 0$. Now, if the distribution of x is $f(x)$, then the probability of a value x to occur is $f(x) dx$, and the probability of a value $(x+r)$ to occur is $f(x+r) dr$. Assuming that the 'event x ' is independent from the 'event $(x+r)$,' the probability of the two events is

$$2 f(x) f(x+r) dx dr. \quad (1)$$

The distribution of r , say $g(r)$, is, of course, the integral of (1) over the range of definition of x , say (α, ∞) , or

$$g(r) dr = 2 dr \int_{\alpha}^{\infty} f(x) f(x+r) dx. \quad (2)$$

As pointed out above, the range is the maximum of the differences $r = |x_k - x_{k+l}|$, $k+l \leq n$. If the form of the distribution $g(r)$ is known, then the statistical theory of extreme values (Gumbel,

1954; Jenkinson, 1955) enables us to find the distribution of the maximum values of r , *i.e.*, the distribution of the range, say R_n , as a function of sample size n . From the point of view of the range R_n , $g(r)$ is the 'parent' or 'initial' distribution. A fitting name for $f(x)$ is 'grandparent' distribution (of R_n).

1.2 Let x be the height of sea level. Whether x is positive or negative, it depends on the choice of the zero of sea level. In any case, it can be made positive by a suitable transformation and we shall assume here, for convenience, that x is non-negative. The earlier mentioned 'samplings' of the variable are readings of sea-level height. We assume, in accordance with observational practice, that the readings are taken at equal intervals of time. If for the unit of time we adopt the length of time between two successive observations, then in an interval n units long we shall have n observations (assuming that the observations are taken at the middle of the time unit). Thus, an interval n units long will correspond to a sample of size n .

In looking for an appropriate mathematical representation of the frequency function $f(x)$ for sea level, we note that the behaviour of many of the geophysical variables with probability distributions may be interpreted to exhibit the operation of two opposing factors. One factor is persistence; in any given 'state,' the variable in question tends to remain in it. This factor may be likened to a 'force' which is constant. The second factor strives to keep the variable at, or about, a mean 'state,' so that the farther away the variable is from the mean 'state,' the smaller is the 'force' to keep the variable there. Hence, the second factor acts as a force which varies inversely with distance from a fixed origin such as the mean.

Before we proceed to discuss the form of $f(x)$, it is in order to point out a limitation of the present study. As we consider conditions under which our variable (*i.e.*, the height of sea level) tends to remain about a mean state, our results will not be valid for time intervals of a length significant on a geologic time scale, during which substantial changes in mean sea level may take place. Of the several geophysical processes which are accompanied by a change in mean sea level, climatic variations seem to be the ones occurring most frequently. In the course of the Earth's history, and certainly since the beginning of the Pleistocene epoch, notable variations of climate have taken place during intervals whose length is of the order of 10^4 years and even of the order of 10^3 years. Hence, the results of the present paper will only hold for intervals whose length, in terms of order of magnitude, is 10^2 years at the most.

Returning to the scheme of forces or factors described earlier, Castellani (1950) has shown that if one factor is a constant 'force' and the second factor is a 'force' inversely proportional to the distance from a fixed origin, then the pertinent frequency function is a Pearson Type III distribution ($x \geq 0$)

$$f(x) = \frac{\gamma^{p+1}}{\Gamma(p+1)} x^p e^{-\gamma x}, \quad (3)$$

$\gamma > 0$, $p > -1$, $\Gamma(p+1)$ being the gamma function of argument $(p+1)$.

The above described scheme of 'forces,' due to Castellani, appears to be applicable to the case of random fluctuations in sea level as well, so that we may assume that the frequency distribution of sea-level heights are of the form of (3). We have checked this point by examining sea-level data for Tel Aviv and found (see Section 2, and Fig. 1 in particular) that a Pearson Type III curve well describes the observed distribution.

In (3) the parameters p and γ are linked with the theoretical mean μ and the variance σ^2 about the mean by the following simple equations:

$$p = \frac{\mu^2}{\sigma^2} - 1, \quad \gamma = \frac{\mu}{\sigma^2}. \quad (4)$$

1.3 Since we assume that $x \geq 0$, the symbol α of (2) becomes $\alpha = 0$. With this in mind, inserting (3) in (2) gives

$$g(r) dr = \frac{2\gamma^{2(p+1)}}{[\Gamma(p+1)]^2} e^{-\gamma r} dr \int_0^\infty x^p (x+r)^p e^{-2\gamma x} dx. \quad (5)$$

Depending on p , $p > -1$, whether it is an integer or not, the integral in (5) is either a polynomial or a power series in r , say $P(r)$. Writing A for the constants independent of r ,

$$g(r) = A P(r) e^{-\gamma r}. \quad (6)$$

If positions of sea-level height were independent, (6) would give the distribution of height differences. In general, independence cannot be assumed, but presumably positions read at relatively distant time points can be considered independent. Hence, we should expect that differences in position readings pertinent to relatively distant time points are better represented by (6).

1.4 We now come to a consideration of the question of the range of variation in sea level.

It is known from the statistical theory of extreme values that *the asymptotic distribution of extreme values depends exclusively on the behaviour of the parent, or initial, distribution toward large values of the variable*. As Gumbel (1954: 22) puts it: "The properties of the initial distribution about the median or the small values of the variate are irrelevant. Methusalas do not die of infantile diseases." Now, if the parent distribution is $g(r)$, eq. (6), its behaviour toward large values of r is dominated by the exponential term e^{-r} . We may expect, therefore, that the asymptotic distribution of ranges of sea level should reveal the properties exhibited by the asymptotic distribution of extreme values in samples from the simple exponential distribution

$$\frac{1}{\sigma_r} e^{-(r/\sigma_r)} , \tag{7}$$

σ_r being the standard deviation (= mean) of the distribution of r . Let R_n be the value of the largest member of r in a sample of size n , $E(R_n)$ the expected value of R_n in samples of size n , $\sigma(R_n)$ the theoretical standard deviation of R_n . The asymptotic distribution of the largest values R_n from a parent exponential distribution, eq. (7), possesses the following two remarkable features (see Gumbel, 1954):

(i) the mean $E(R_n)$ increases with the logarithm of sample size according to the formula

$$E(R_n) = \sigma_r \ln n + \frac{\sqrt{6}}{\pi} C \sigma(R_n) , \tag{8}$$

C being Euler's constant, $C = 0.5772 \dots$

(ii) $\sigma(R_n)$ is independent of n , say, $\sigma(R_n) = \sigma_R$; moreover

$$\sigma_R = \frac{\pi}{\sqrt{6}} \sigma_r . \tag{9}$$

In view of the above we should expect the range of sea level to increase with the logarithm of sample size ($\sim$ time) and the standard deviation of ranges in samples of size n to be constant, apart from errors of sampling.

1.5 In practice, we do not have the theoretical values of $E(R_n)$ and of σ_R (or of σ_r). Nor will the standard deviation of the observed range, say $s(R_n)$, in samples of relatively small size represent the asymptotic value of the standard deviation. The best we can do in (8) is replace $E(R_n)$ by the sample average $\bar{R}_n$ of the observed largest values, replace $\sigma(R_n)$ by $s(R_n)$ or by $\bar{s}_R$ if $s(R_n)$ is sensibly

constant with n , and then estimate the term $\sigma_r \ln n$ in (8) from the equation

$$\sigma_r \ln n = \bar{R}_n - \frac{\sqrt{6}}{\pi} C s_R. \quad (10)$$

In place of the true sample size n , we shall often have to choose an arbitrary sample size n' , say, such that

$$n = k n'$$

$$\ln n = \ln n' + \ln k,$$

k being a constant (possibly unknown). Hence, using n' in lieu of n merely introduces in the equation an additional *constant* term, or, writing n for n' ,

$$\begin{aligned} \sigma_r \ln n &= \bar{R}_n - \left(\frac{\sqrt{6}}{\pi} C s_R + \sigma_r \ln k \right) \\ &= \bar{R}_n - B, \text{ say.} \end{aligned} \quad (11)$$

Putting $n = 1$,

$$B = \bar{R}_1;$$

that is to say, we estimate B from the average range of the samples whose size we arbitrarily take to be 1.

2. OBSERVATIONS

2.1 To check on the validity of inferences drawn in Section 1, we have examined data of sea level for Tel Aviv. The data are hourly observations of a tide gauge at the Reading Power Station (32° 06' N, 34° 47' E) of the Palestine Electric Corporation Ltd. Excepting January and February 1944 and October 1953, the data are almost complete since June 1943 through April 1955, *i.e.*, the data cover 12 years less 4 months. Fig. 1 is a histogram of the combined data for January and July of the five years 1950–1954, the number of observations actually taken being 7307. It is seen from the diagram that the distribution is bell-shaped though slightly asymmetric. The mean, relative to an arbitrarily fixed zero, is at 51.9 cm, while the standard deviation is 16.3 cm. Taking these observed values as the best estimates of the corresponding theoretical quantities, the parameters p and γ of (3) work out, in accordance with (4), as follows:

$$p = 9.137, \quad \gamma = 0.196. \quad (13)$$

The frequencies computed from (3) and (13) are also plotted in

Fig. 1. It is obvious that (3) represents the observed distribution quite well. We should expect, therefore, that the range of sea level increases with the logarithm of sample size.

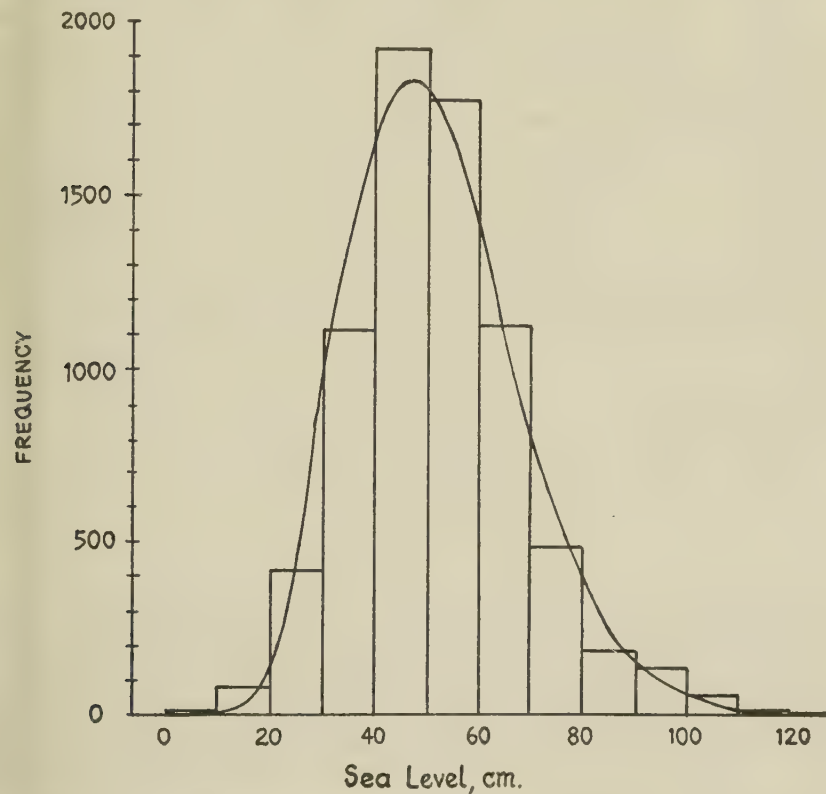


Figure 1. Distribution of sea-level heights at Tel Aviv, January and July 1950-1954. Histogram: observed distribution; curve: Pearson's Type III.

2.2 Table I summarizes the results obtained from the Tel Aviv data. Column (C) is the average of the ranges for intervals whose length is stated in column (A). The number of such intervals available is shown in column (B). Column (E) states the sample size. If we consider an interval one month long as the unit of time and disregard the slight differences in the lengths of months, then its sample size may be taken as 1. In this case, the sample size of an interval one year long is, of course, 12. Since we choose the month as our unit sample size, we take, in accordance with what was said in connection

TABLE 1. AVERAGE RANGES OF SEA LEVEL AT TEL AVIV (JUNE 1943 THROUGH APRIL 1955) AS A FUNCTION OF LENGTH OF TIME INTERVAL

(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)
Length of interval	No. of intervals available	Average range (cm)	Standard deviation of range (cm)	Sample size, n	ln n	$\hat{\sigma}_r$ [eq. (14)]	Range computed from eq. (15)
One month	140	70.7	15.7	1	0	(15.7)	70.7
Two months	69	81.1	15.5	2	0.693	15.0	81.3
Three months	45	86.1	14.8	3	1.099	14.0	87.5
Six months	21	100.1	16.4	6	1.792	16.4	98.1
One year	12	109.6	15.4	12	2.485	15.7	108.7
Two years	6	118.0	14.8	24	3.178	14.9	119.3
Four years	3	126.6	—	48	3.871	—	129.9
Six years	2	138.5	—	72	4.277	—	136.1
Twelve years	1	147.0*	—	144	4.970	—	146.7

* As this figure is based on a single sample, its agreement with the figure computed from eq. (15) must be considered accidental.

with (11) and (12), $\bar{R}_1$ (i.e., the average monthly range) for the estimate of the constant B .

Column (G) of Table I gives the term

$$\frac{\bar{R}_n - B}{\ln n} = \frac{\bar{R}_n - \bar{R}_1}{\ln n}, \quad (14)$$

which by (11) should give us an estimate, say, $\hat{\sigma}_r$ of σ_r . Actually, an estimate of σ_r could be obtained by considering the distribution of the differences $|x_k - x_{k+l}| = r$ of the original sea level data. However, this would involve considerable computational labour and for this reason we take the average of column (G) for the estimate of σ_r . It is seen that the figures in that column show little scatter about their average 15.3. Thus we are led to estimate the range of sea level from the equation

$$\begin{aligned} \bar{R}_n &= 15.3 \ln n + 70.7 \\ &= 35.2 \log_{10} n + 70.7. \end{aligned} \quad (15)$$

The ranges computed from (15) are listed in column (H). Because of the little scatter in column (G), it is natural that the figures in column (H) are in close accord with the observed figures, column (C). The observed and computed ranges are also shown in fig. 2.

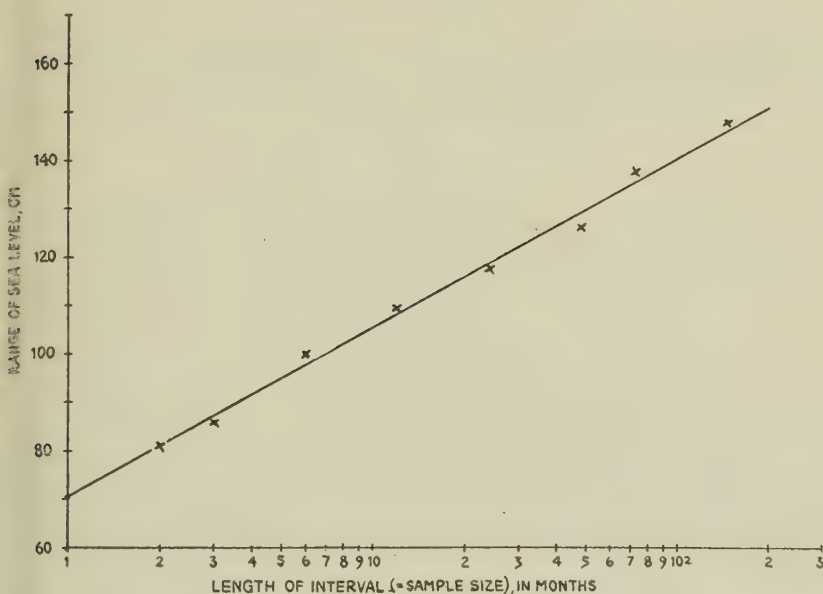


Figure 2. Variation in range of sea level with length of interval. Crosses: observed ranges; straight line: eq. (15).

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FLUCTUATIONS IN POPULATIONS OF LITTORAL MARINE INVERTEBRATES

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ABSTRACT

Fluctuations in populations of various species of marine invertebrates, several of them over many years, are recorded. Some of the data are quantitative, but most of them are merely estimates of relative abundance at the same season in successive years. Records of local fluctuations in populations of the Pismo clam extend over 25 years, those of dinoflagellates 20 years, and of *Donax* 58 years; records of the set of young oysters cover 70 years and those of the local production of oysters 100 years. These data offer no satisfactory evidence of persistent rhythmical periodicity in any of the species. Changes that have occurred in local populations of littoral invertebrates due to constantly changing environmental conditions and to the introduction of foreign species during the past half-century are recorded. Some of these changes have been catastrophic.

INTRODUCTION

The term annual fluctuation is used in this report to designate variations in the relative number of individuals of a particular species in the same locality in successive years. The estimated amount of fluctuation is based on samples which have been taken at the same season each year in order to avoid the complication of seasonal variations, which are often of considerable magnitude. The number of individuals usually have been largest shortly after periods of reproduction. Fluctuations have varied simultaneously in different parts of the range of a species, since they are largely dependent on local environmental conditions, including diseases.

The writer has recorded many observations of changes which have taken place in populations of various species of littoral invertebrate during the past half-century along the coasts of southern New England and southern California. Most of these changes have been minor fluctuations in numbers while others have been catastrophic, with the total elimination over considerable areas of all members of sus

¹ Contributions from the Scripps Institution of Oceanography, of the University of California. New Series, No. 940.

ceptible species or even of the entire littoral fauna. Catastrophic changes have obviously resulted from wide deviations in environmental conditions or from diseases, but no satisfactory explanations have been found for many of the observed fluctuations.

ANNUAL FLUCTUATIONS

Kemp (1938), Dexter (1944), Burkenroad (1946) and many others have published numerous examples of fluctuations among marine invertebrates, and others are known to every naturalist who is acquainted with the seashore.

At present many long-term records are available. Some of these are quantitative or semiquantitative in nature, while others are mere estimates of relative abundance which record whether many, few or none of a species were present. Some of these records were obtained in a survey of a particular locality at the same season in successive years. Some have reference to the entire local population of a species and others to only a single year-class. Also, annual records of the production of some commercial species are available for a long series of years. It seems desirable to examine a few of these records in order to determine the magnitudes and intervals observed.

1. Pismo Clam.—In the population of the Pismo clam (*Tivela stultorum*) at La Jolla, California, changes which occurred in each year-class during five successive years (1945–1949) were determined by collections taken at monthly intervals, beginning at the time when the young clams first appeared on the beach. Of the average total of 297 individuals found on a restricted portion of the beach in September of these years, 214 were in the first year-class, 71 in the second, 8 in the third, and 4 in the fourth. The population on the beach in those five years indicated that there was an annual loss of 67 to 75% for each year-class and that less than 1% of the young individuals reached the age of four years (Coe, 1947; Coe and Fitch, 1950). A few individuals of more than 20 years of age have been found on the same beach.

Fig. 1 shows not only the number of individuals in each year-class at the end of September from 1945 through 1949 but estimates of the total population from 1938 to 1952 as well. It will be observed that the number of those one year of age increased rapidly in 1946 and decreased in 1949, that those aged two years increased in each successive year, and that the reduced populations of older clams remained nearly stationary. The estimated total population increased about six-fold during the five years preceding 1943. This

was followed by a considerable decrease in numbers, with a resurgence in 1946. From 1949 through 1952 there was a rapidly declining population because of the failure of young clams to establish themselves on the beach at the end of the free-swimming larval periods. In 1953 the species had disappeared almost completely from the intertidal zone, not only locally but also in other formerly well populated areas. No significant deviation from average in temperature or salinity and no evidence of disease have been observed. Although some of the larger individuals were taken by poachers, it is concluded that deviations in the currents along the coast were mainly responsible for this pronounced decline. The larvae apparently have a pelagic

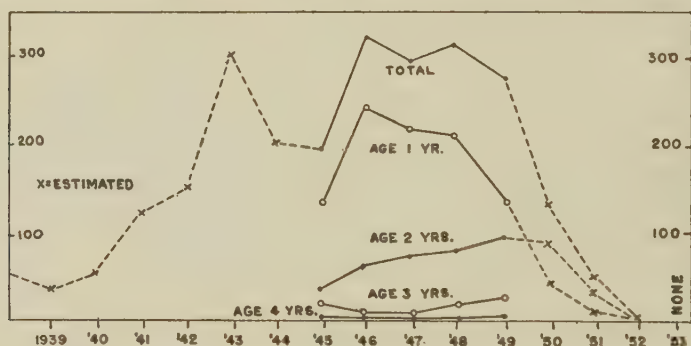


FIGURE 1. The constituent year-classes in the Pismo clam population on a restricted portion of the beach at La Jolla, California, during the last week in September of each year, 1938-1953. The numbers indicated for 1945 through 1949 are strictly quantitative and indicate an annual mortality rate of 67 to 75%. The total mortality from the first to fourth years was 97.5%. For the other years the population is estimated. No new set arrived in 1951 and the entire population disappeared in 1952.

life of two to three weeks or more, and during this period they may be carried far from their place of spawning by the ocean currents which on that part of the coast have an average velocity of four to five miles a day. Consequently the young clams in any locality may originate from populations living several, or even many, miles distant and the larvae are dependent upon favorable currents to bring them to the beach at the exact time when they are ready for transforming and settling in the sand. Presumably diseases similar to those recorded in this paper for *Donax* and oysters were responsible for many deaths; however, the causative agents were not determined. In some localities, every large clam observed showed macroscopic evidence of disease; some were moribund and others had died recently.

The greater range in the fluctuations of the young as compared with older individuals is shown in the records of the Pismo clam

populations at Pismo Beach, California, for the years 1923 through 1950. The samples were standard in that the same areas of the beach were covered in November of each year. The constituents of this population were described by Coe and Fitch (1950) but several of the data require further analysis. The first year-class is of particular interest. The numbers of young clams which settled in the measured areas and survived until the census was taken each year are shown in Fig. 2. The figures indicate variations ranging from 0 in 1934 and 1950, 1 in 1949, 6 in 1928, and 9 in 1938 to 743 in 1937, 758 in 1935, and 871 in 1931. The total of 4111 in the first year-class

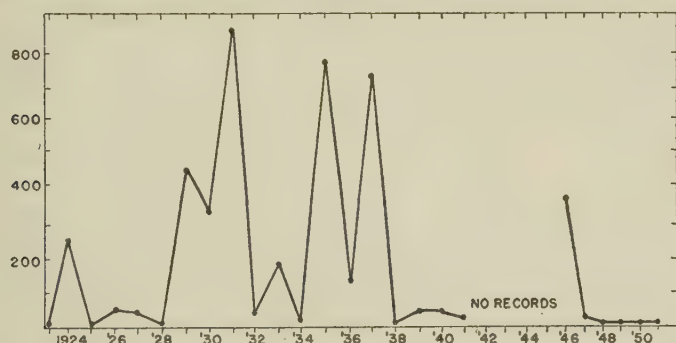


FIGURE 2. Fluctuations in the first year-class of Pismo clams at Pismo Beach, California, estimated from samples taken in November of each year by the California Bureau of Marine Fisheries. An increased population in alternate years as compared with each preceding year was of general occurrence.

during the 19 years was 50% of the entire population not exceeding four years of age. Thus a high rate of mortality is indicated.

It will be noted that during most of this period there was a biennial rhythm in the set or survival of young clams, the numbers in each alternate year being greater than those in the preceding year (Fig. 2). It seems possible that this may have been a chance occurrence due to variations in the water currents, but why there should have been five years in succession with no appreciable set on this beach remains unexplained (Fitch, 1952).

In order to avoid the possible influence of strictly local fluctuations, the collections were made in three well separated sections of the long beach (Fig. 3). The Pismo section was 1.4 miles from the Oceano section and 6.5 miles from the Le Grande section. The data compiled by Fitch (1952) show that, in spite of the distances separating the three sections, the fluctuations were generally parallel at each date of sampling (Fig. 3). This is presumably indicative of nearly uniform

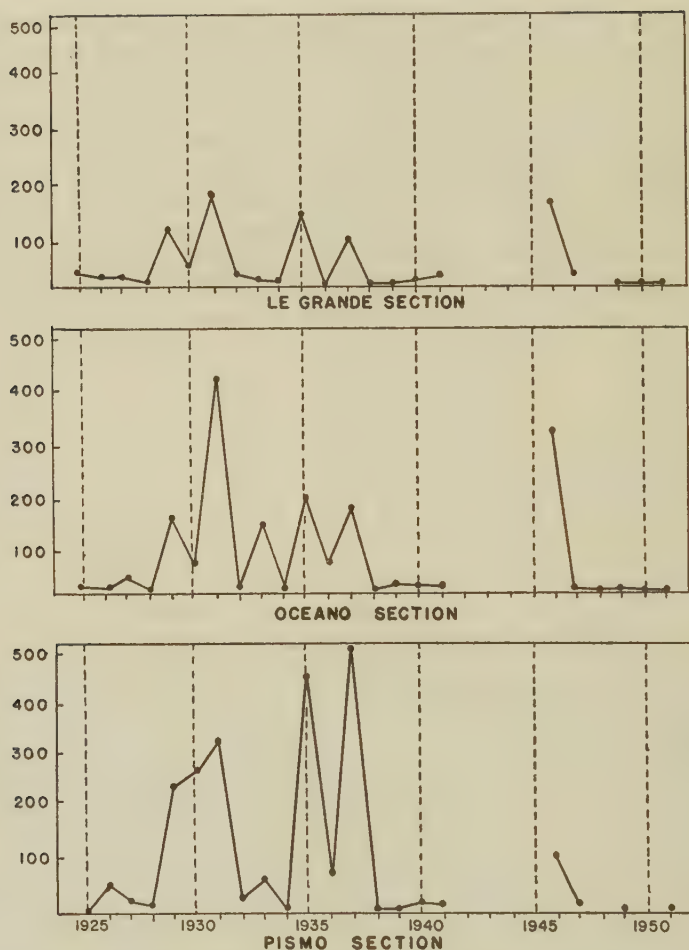


FIGURE 3. Fluctuations in the numbers of young Pismo clams found in the three sections of Pismo Beach, California, in November of the years 1925 to 1951, with the exception of 1942-1945. The same areas were covered each year. In all three sections, which were from 1.5 to 6.5 miles apart, each alternate (odd-numbered) year previous to 1940 generally showed an increased set as compared with the immediately preceding and following year; but in 1946 the trend was reversed. From 1946 to 1952 the set has been extremely small. Data from Fitch (1952).

environmental conditions along the entire extent of the beach in any given year although such conditions undoubtedly varied in different years.

The life span of individuals of this species may exceed ten years

under favorable conditions, and each adult female may produce from 5 to 20 million eggs annually. During the years in which practically no young appeared there were many thousands of adults on the same beach, hence it is concluded that the immense numbers of potential young either failed to survive or were carried to other beaches, perhaps some miles distant. Presumably a large proportion of the young perished by being carried too far from shore; Johnson (1940) found larvae of the sand crab *Emerita* more than 90 miles from the nearest coast although the adults live only in the intertidal zone. Some were undoubtedly devoured, some probably died because of adverse temperature or lack of suitable nutrition, and possibly others succumbed to parasitic disease either before or after setting.

The older year-classes were less variable in numbers, the second year-class fluctuating from 2 in 1935 to 297 in 1947, the third year-class from 3 in 1946 to 245 in 1937, and the fourth year class from 4 in 1930 to 200 in 1946.

2. Oysters.—A quantitative study of variations in the number of young oysters (*Crassostrea virginica*) which set on 100 oyster shells in Long Island Sound has been made by Dr. Victor L. Loosanoff during 15 summers, 1937 through 1951, and by his permission the unpublished data are shown in Fig. 4. It will be noted that in two



FIGURE 4. Yearly variation in the average set of young oysters on 100 oyster shells placed at various depths. Long Island Sound. Unpublished data supplied by Dr. V. L. Loosanoff.

of these years the numbers were 40 times greater than those in the preceding year and were correspondingly larger than any set during the last five years. It appears that the number of survivors which reached the places for attachment fluctuated widely, but there is no evidence as to the number of larvae produced.

The longest continuous record concerning fluctuations in popula-

tions of any American marine invertebrate may be found in the estimates of the relative abundance of the set of young oysters in the large oyster producing areas in Long Island Sound. It is obvious that a heavy set is generally, but not always, indicative of a large future population of adults. These records for the past 70 years have been compiled by Loosanoff and Engel (1940) and have been supplemented by personal communications from Dr. Loosanoff. Fig. 5 indicates that heavy sets were reported in 12 of the 18 years prior to 1900 whereas in only six years of the present century has the set been considered heavy. From 1906 to 1924 there were continual failures and light sets; medium sets occurred in 1926, 1934,

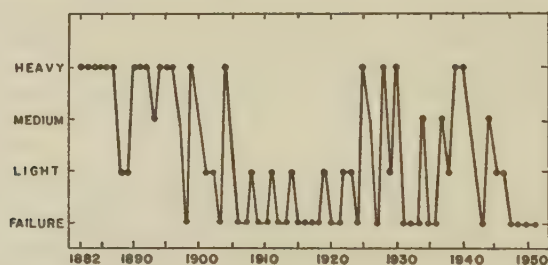


FIGURE 5. Fluctuations in the estimated set of young oysters in Long Island Sound during the past 70 years. Heavy sets were common in the years preceding 1900 and again in 1925 to 1929, but there were only light sets or failures from 1906 to 1924 and from 1945 to 1951. Data from Loosanoff and Engle (1940) and personal communications.

1937, 1941 and 1945, and heavy sets in 1904, 1925, 1928, 1930, 1939 and 1940.

Note that in four of these years heavy sets occurred in the year immediately following one in which the set was a failure and that in only one year (1931) did a failure occur immediately following a heavy set. A sequence of six heavy sets was reported at the beginning of the record and a sequence of four failures followed 1914. In other years a maximum of three heavy sets or four failures followed in sequence. A cyclical periodicity in abundance is not evident. It is obvious that a light set accompanied by a low rate of mortality may be more productive than a heavy set with high mortality.

3. Starfish.—A quantitative study of the variations in the rate of attachment of young starfish (*Asterias forbesi*) on planted oyster shells for the years 1937 through 1951 was made by Dr. Loosanoff, who has kindly supplied the data indicated in Fig. 6. It will be seen that the numbers were much larger in 1938 and 1941 than in more recent years. It was mentioned in a preceding paragraph that the

associated set of young oysters was also much reduced in the five most recent years.

A cyclical periodicity has been reported by Burkenroad (1946) for the same species of starfish. From an examination of published reports of the oyster industry, of newspaper accounts and of testimony of oyster growers, he concluded that this starfish, which is the chief enemy of the adult oyster on the southern coast of New England, has been particularly destructive at intervals of about 14 years during the past 90 years. To Burkenroad the records seemed to indicate an interval of approximately 7 years between the periods of minimum and maximum abundance in each cycle. It seems doubtful, however,

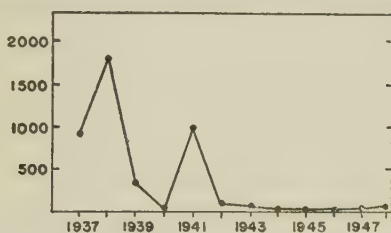


FIGURE 6. Fluctuations in the average seasonal set of young starfish on 100 oyster shells placed at various depths in Long Island Sound in the years 1937-1948. Unpublished data supplied by Dr. V. L. Loosanoff. The graph shows young populations in 1938 and 1941 which were many-fold larger than those in subsequent years.

whether the data from the diverse sources mentioned, although of much interest, are sufficient to justify the conclusion that such definite periodic cycles prevail. He estimated that the population at peak periods might be 20 times that at trough periods.

The term "Resurgent Populations" is appropriately used for such populations as experience only minor fluctuations for a number of years and then increase rapidly to many times their former numbers with an increment of a hundred or even thousands. After one or several years of increase the population usually returns to approximately its former size. Such a resurgent population for the Pismo clam is shown in Fig. 1 and for the mussel *Septifer bifurcatus* in Fig. 2. Every naturalist familiar with seashore life must have noticed such resurgent populations, for they are common to all groups of invertebrates. A species formerly considered scarce suddenly becomes abundant and soon becomes scarce again.

4. *Donax*.—Conspicuous examples of this type of population are found in certain species of the little "bean clam," *Donax*. Of the two

species found in California, *D. californica* usually occurs only in small populations while *D. gouldii* remains relatively scarce locally for a number of years and then appears in countless millions. At such times the shells lie in contact or even in several layers in the intertidal zone over many miles of the sandy beaches.

After a life span of three years or less, the clams have sometimes disappeared so completely that not a single individual could be found in the intertidal zone on an extent of beach which was occupied by millions a few months earlier. Fig. 7 shows that these resurgent populations have been recorded at La Jolla in 1894-95, 1909-10, 1913-15, 1931-32, 1934, and 1937-38.

During the summer of 1949 there arrived a resurgent population

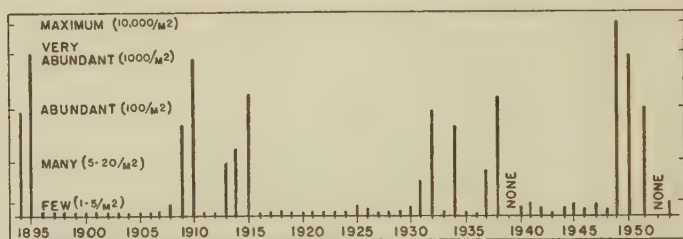


Figure 7. Resurgent populations of *Donax gouldii* in the intertidal zone at La Jolla, California. Estimated relative abundance: "few," less than 5 per square meter; "many," 5 to 20; "abundant," more than 100; "very abundant," more than 1000; "maximum," more than 10,000 per square meter. The populations in the years preceding 1926 and from 1927 to 1936 are estimated from the incomplete records by Dr. W. E. Ritter, Mr. Percy Barnhart, and others; those of 1926, 1927, 1937 and subsequent years are from personal observation by the writer. The entire populations died in 1939 and in 1952.

which seems to have been of unprecedented magnitude. In the autumn of that year the beach had an average population of more than 20,000 young clams per square meter in a zone 2 to 5 meters wide which extended with some interruptions for more than five miles along the coast.

This dense population continued, but with considerable mortality for almost two years. In July 1951 approximately half of the individuals died after spawning, but those remaining still formed a dense population in many areas. As soon as spawning began the following spring the mortality increased until about mid-July 1952, when only about 20 individuals per square meter, 0.1% of the early population remained. The major portion of the mortalities occurred within a few days. The deceased included not only members of the resurgent population, which had then attained the ripe old age of nearly three years, but also most of the younger individuals which had reached the beach in the two intervening years and which had managed to

survive in less crowded situations until the final catastrophe. Extended search along the beach, both in the intertidal zone and below, failed to reveal a dozen individuals, old or young, excepting one small area in which all members of the resurgent population died; the younger year-classes survived a few months longer. The miles of sandy beaches thickly strewn with empty shells bore vivid testimony as to what had occurred.

Samples of the population had been examined microscopically once each month or oftener throughout the 3-year history of this phenomenon. Infestation with trematode parasites was common, but no evidence of truly pathogenic organisms appeared during the last two years. Thereafter the moribund individuals lay fully exposed on the surface of the sand for several days before death, apparently too feeble to bury themselves after having been washed out by the surf. The bodies were thin and watery, often with greenish exudations of blood and blood corpuscles, together with many minute unicellular parasites in the connective tissues, blood vessels, epithelium of gut and other tissues. On this evidence it is presumed that the minute parasites caused the epidemic.

In the year preceding this resurgence the population did not exceed one clam per square meter in the same area, although it is probable that some individuals were present below the tidal zone. It is not known whether this resurgent population originated from these few local individuals or were brought as larvae from a distance of many miles by ocean currents, as mentioned earlier. During the months preceding the appearance of this resurgent population at La Jolla there were populations of spawning adults at Coronado, about 12 miles south, at Sunset Beach, 65 miles north, and probably at other localities along the coast. With favorable current velocities of 2-5 miles per day, the larvae could have reached La Jolla from either of these localities during the larval period.

The occasional occurrence of these resurgent populations is presumably due to the chance combination of suitable conditions during the pelagic larval period and to favorable currents which bring the swarms of larvae to the beach at the exact time when they are ready for transforming and setting.

5. Mussels.—Not infrequently an introduced species multiplies with great rapidity for a few years and then declines or disappears. The bay-mussel (*Mytilus edulis diegensis*) offers an excellent example of the rise and fall of such a newly arrived population. In 1940 this subspecies attracted considerable attention in Newport Bay, California, because of its great abundance, and three years later, in August

1943, a small colony was found on the pier at the Scripps Institution of Oceanography, about 60 miles south of Newport Bay. Within a few months they multiplied so that by the following summer these mussels covered all available spaces in the intertidal zone on the pier as well as on adjacent rocks. Later they were found in Mission Bay, San Diego Bay and elsewhere along the coast, and soon they became a nuisance by clogging the intake pipes of salt-water systems. In many situations there were so many young that they could not possibly have grown to maturity because of lack of space. Thus

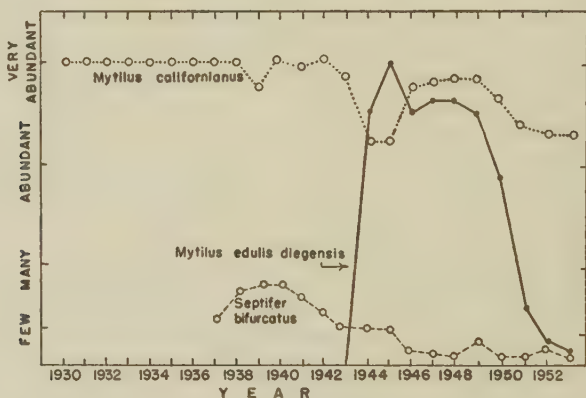


FIGURE 8. Comparison of populations of three species of mussels on the pier and rock at La Jolla, California. The bay-mussel (*Mytilus edulis diegensis*) represents the temporary exuberance of a newly introduced stock. The sea-mussel (*Mytilus californianus*) has maintained an essentially maximum population with only minor fluctuations except in the years when the bay-mussel pre-empted the more favorable situations or when starfish were unusually numerous. The population of the ribbed mussel (*Septifer bifurcatus*) has been sparse except for a slight resurgence in 1938 to 1940.

vast colonies sprang up in situations unsuitable for long survival (Coe, 1946). Following the maximum during the second year after arrival, the numbers diminished slightly and then declined rapidly to a relatively sparse population in the seventh year (Fig. 8).

In contrast with this briefly exuberant population, the native sea-mussel (*Mytilus californianus*) has long maintained maximum numbers, with only small fluctuations except for the years when many of the situations suitable for attachment of the young were pre-empted by the bay-mussel (Fig. 8).

A third species of mussel, *Septifer bifurcatus*, which occupies the same habitat, has maintained a sparse population except for a brief resurgence from 1938 through 1942 (Fig. 8).

6. Dinoflagellates.—Since the productivity of the sea is so largely dependent on phytoplankton for the nutrition of marine animals, it would naturally be expected that conditions favoring large phytoplankton populations would likewise be associated with large animal populations. An abundant crop of phytoplankton is normally accompanied by a large crop of grazing zooplankton which in turn serves directly or indirectly as food for larger animals, invertebrates as well as vertebrates. Thus the phytoplankton primarily, together with other marine plants and a comparatively small amount of detritus from the land, supplies the nutrition of all marine organisms. Hence if a rhythmical periodicity actually occurs in the production of phytoplankton over a series of years, associated changes in the animal populations should be predictable.

Statistical studies by Allen (1941) on the abundance of dinoflagellates on the coast of southern California, extending over a period of 20 years, have shown that the populations of dinoflagellates indicate an inverse correlation with the temperature of the water during the first quarter of the year. Low temperatures on that portion of the Pacific coast often indicate upwelling of deeper oceanic water which brings with it phosphates and other inorganic nutrients required for the growth of phytoplankton and animals. His data, however, do not show satisfactory evidence of cyclical periodicity.

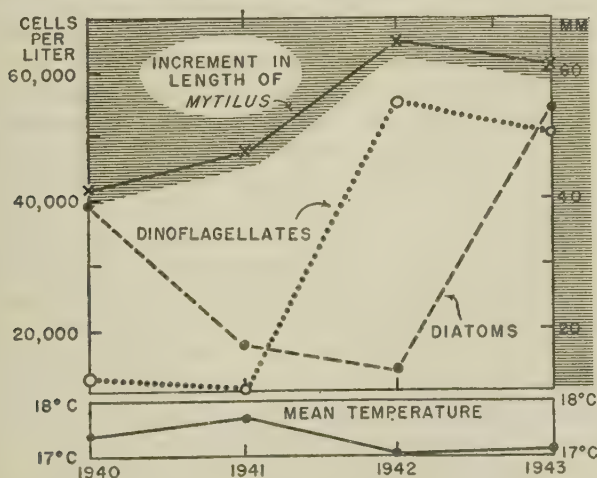


FIGURE 9. Fluctuations in the populations of diatoms and dinoflagellates as correlated with mean annual temperature of the water and increment in growth rate of mussels at the Scripps Institution of Oceanography, La Jolla, California. Low average temperature is associated with upwelling oceanic water, with large populations of dinoflagellates and relatively few diatoms, as well as with rapid growth of mussels.

In studies from 1940 through 1943, Coe and Fox (1944) found that the largest dinoflagellate populations occurred during 1942 when the lowest annual water temperature was recorded and that there was a more rapid growth of mussels in the same locality in 1942 than in the three years of higher temperatures. On the other hand, the populations of diatoms in 1942 were smaller than those of the other three years (Fig. 9).

CATASTROPHIC CHANGES

The littoral fauna, in contrast with fauna of the open ocean, is subject to great vicissitudes. During the half-century under observation there have been occasions when excessive cold in winter or heat in summer has destroyed all or nearly all individuals of susceptible species of the population over large areas.

Along the coast of southern New England during certain winters, particularly that of 1918, extensive populations of invertebrates were killed when the intertidal zone was exposed to temperatures far below the freezing point of sea water. Allee (1923) has shown that species having a more southerly range suffered greater losses than those which have a normal range extending farther northward. Blegvad (1929) described the high mortality among littoral invertebrates along the northern coasts of Europe during unusually cold winters. Heat combined with excessive salinity often produce similar catastrophes, as Gunter (1947) observed in the Gulf of Mexico.

MacGinitie (1939) has reported that the heavy rains and freshets of 1927, 1938, and 1941, and presumably of other years, lowered the salinity of the water in some of the bays along the coast of southern California to such an extent that only the more tolerant invertebrates in the intertidal zone were able to survive.

Severe storms and violent surf have in many winters washed out the intertidal substrate, thus destroying the associated invertebrates or crushing them as the surf pounded the rocks on or beneath which they had maintained flourishing colonies.

Epidemics of parasitic diseases have destroyed populations of sponges, oysters, clams, mussels and other invertebrates along many miles of seacoast within a single year. The epidemics in the bay clam, *Donax*, at La Jolla, California have been mentioned earlier. Diseases of an apparently similar nature, which have been destructive to oysters on the southern Atlantic and Gulf coasts of the United States in recent years, have long been known from other parts of the world (Mackin, 1951).

Sedentary invertebrates with a pelagic larval life are subjected

to great vicissitudes because of their dependence upon favorable currents, as noted earlier. On both the Atlantic and Pacific coasts adverse currents have evidently caused the complete failure of young oysters and clams to establish themselves in many formerly populous localities.

Many marine invertebrates are more or less dependent upon vegetation for support or protection, and without it they perish. Mention may be made of the bay scallop (*Pecten irradians* = *P. gibbus*) which formerly lived in vast colonies in eelgrass (*Zostera marina*) in protected areas over a great extent of the Atlantic coast. Though not limited to such situations, the scallop populations suffered a rapid decline in numbers in 1931-1933 following destruction of the eelgrass by disease. A lucrative fishery disappeared in many localities. With the scallop went also many of the ophiurans, annelids, nemerteans, echiuroids, crustaceans, bivalves and other invertebrates that had found congenial homes in and beneath the vegetation. In some areas, however, the populations of scallops have more recently increased again in spite of the absence of eelgrass (Marshall, 1947).

The most spectacular catastrophes to both invertebrates and vertebrates along many miles of seacoast have been caused by a sudden heavy bloom of poisonous dinoflagellates, commonly referred to as "red water." These phenomena occur frequently in areas of upwelling. Brongersma-Sanders (1948) has shown that on some coasts they may be expected annually but that in most regions they occur at irregular intervals and cannot be predicted.

On the coast of southern California red tide has been observed either locally or over an extent of 100 to 200 miles or more in 1894, 1901, 1907, 1917, 1924, 1933, 1938, 1939, 1945 and 1952; thus the intervals have been 7, 6, 10, 7, 9, 5, 1, 6 and 7 years, with an average of nearly 6.5 years. Some of these occurrences have been highly destructive to both vertebrates and invertebrates while others have caused little injury. Although several species have been involved, the greatest destruction occurred when *Gonyaulax polyhedra* was the predominant organism. Not infrequently in years other than those noted above, the water has become more or less distinctly discolored locally in midsummer by populations of species of *Prorocentrum*, *Ceratium* and other dinoflagellates, but the populations did not reach the density characteristic of red water.

There are many records of the rapid elimination of flourishing populations due to pollution by oil and industrial wastes. Harbors and estuaries which formerly supported a vast assemblage of invertebrates have become barren wastes except for a few of the more resistant species. The effluent from sewers of certain communities, however,

supplies additional nutrition for bivalve mollusks and other forms which feed on particles in suspension.

INTRODUCTION OF FOREIGN SPECIES

Some of the populations under observation have maintained themselves for many years with relatively little apparent change while others have fluctuated widely. Certain mussel beds, for example, with their associated invertebrates, have the same appearance today as they had 50 years ago whereas others have disappeared completely or have disappeared and repopulated repeatedly.

With few exceptions the species that constitute the marine invertebrate fauna of southern New England today are the same as those that were reported by Verrill (1873), although they have varied greatly in local abundance during the past 80 years. New species have been described each year, but most of these have been inconspicuous creatures that Verrill did not study or did not find. Changes in the local distribution of some of the species have been profound, due in large measure to the increased demand for seafood, the encroachment of industry, and the development of seashore properties, but none of the species appears to have been exterminated. Only three conspicuous species have become common since the publication of Verrill's report. The edible periwinkle (*Littorina litoria* L.) of European coasts was first noticed at Woods Hole in 1875 and soon became abundant along the coast as far south as Virginia. Another conspicuous, and sometimes abundant, species not reported by Verrill is the medusa *Gonionemus murbachi* Mayor; this was first found in the Eel Pond at Woods Hole in 1894. The sea-anemone *Aiptasiomorpha* (*Sagartia*) *luciae* (Verrill), discovered in 1887 on the southern coast of New England, became one of the most abundant constituents of the littoral fauna as far south as Florida and the Gulf of Mexico; it has fluctuated widely in abundance and local distribution in subsequent years.

Frequently the result of the introduction of a species of marine invertebrate, either accidentally or intentionally, into a foreign locality has been its speedy elimination. Even when environmental conditions seemed suitable for the existence of introduced individuals, conditions have seldom been favorable for reproduction and continuation of the species. Hence most of the attempts to introduce useful marine invertebrates have met with failure, but there have been some exceptions; a few of the useful species have been successful in establishing themselves in their new environments and have supplemented the human food supply.

The accidentally introduced Japanese little-neck clam (*Protothaca philippinarum*, also known as *Tapes semidecussata*) is an example. This highly palatable bivalve was first noticed on the coast of British Columbia in 1936. During the ensuing eight years it spread widely and in 1944 it had extended along the coast for a distance of more than 80 miles. It is stated by Neave (1944) that in some areas only two seasons of spawning were required to make it more abundant than any of the edible species of native clams. The species is now established at many localities along the Pacific coast and has become commercially important.

The intentional introduction of the soft-shell clam (*Mya arenaria*) of the Atlantic coast furnished the stock from which large crops of these succulent bivalves are now harvested commercially each year in many areas on the Pacific coast. Other introductions from the Atlantic to the Pacific include the horse mussel (*Voltsella demissa*) and the quahog (*Venus mercenaria*). The snails *Ilyanassa obsoleta*, *Crepidula plana*, *C. glauca*, *C. fornicata*, *Busycon pyrum* and the gem clam (*Gemma gemma*) are among the immigrants who were transported from east to west coasts as stowaways among oysters.

Attempts to establish reproductive colonies of the Atlantic oyster (*Crassostrea virginica*) on the Pacific coast have not generally met with success; however, when the spat has been introduced it has grown to maturity in some localities, and it is said that normal reproduction occurs occasionally. Plantings of the lobster from the Atlantic coast have always failed.

Only a single species of marine invertebrate has been transported intentionally across the continent in the opposite direction, the reason being that edible invertebrates of the Atlantic coast are almost invariably more succulent than their relatives of the Pacific. Experimental plantings of the Japanese oyster have been made on the coast of New England in the hope that this species will thrive in situations that are unfavorable for the growth of the superior native species.

For many years on the Pacific American coast the Japanese oyster (*Crassostrea gigas*) has been successfully cultivated from young imported each year from Japan. This procedure has been necessary because of its failure to reproduce in the new localities. More recently, however, normal reproduction has occurred in certain areas at intervals of a few years, but most of the commercial crop is still grown from the imported young.

Unless great care is exercised there is always danger of introducing harmful species with beneficial species, and the former sometimes multiply more rapidly and prove to be even more injurious than they

were in their native home. For example, in its native southern New England habitat the snail *Crepidula fornicata* is only occasionally injurious to the oyster beds, but on both shores of the English Channel it has become a great nuisance since it was accidentally introduced with American oysters. The snails quickly established themselves but the oysters did not. The boring snail or drill (*Urosalpinx cinerea*) which is so destructive to oysters and other bivalves, was brought to the Pacific coast and to the coasts of England in futile attempts to introduce oysters from the American Atlantic coast. The similarly destructive Japanese drill (*Tritonalia japonica*) has also become established on the American Pacific coast. The barnacle *Elminius modestus* from the southern hemisphere has now become a pest on British oyster beds, and species of *Teredo*, *Bankia* and *Limnoria* which destroy wooden marine structures, have established themselves on all sea coasts except in the far north and far south.

PRODUCTION RECORDS

A summary of the commercial production in the various groups of marine organisms may be found in "Marine Products of Commerce" by Tressler, *et al.* (1951). However, these records of production do not afford reliable evidence as to the relative size of the population in any year or in any locality because they are influenced in large measure by economic factors such as demand, price and available manpower. Thus, from such records it may appear for a limited time that production is increasing when the population is actually being rapidly depleted. Records of oyster production in Maryland for more than a century, published by Beavan (1945), are typical of the production of most other invertebrates of economic importance. During the periods of maximum production between 1875 and 1899, 10 to 15 million bushels were harvested in that area annually. Then during the ensuing 13 years the rate of production declined rather rapidly, and more recently it has fluctuated irregularly between 1 and 3 million bushels a year, or one-fifth the previous maximum. In this case the production has been correlated with the size of the oyster population, since both have declined to about the same extent.

In most of the other oyster-producing areas on the Atlantic and Gulf coasts there has been a somewhat similar decrease in the past quarter century, but there have been some exceptions, such as that in Louisiana where the annual production has fluctuated widely but where there has been no downward trend during the 20 years preceding 1949 (Gunter, 1949).

Recently the commercial production of the various species of clams in most areas has declined even more rapidly than the production

of oysters. On the contrary, lobster production in the New England and Middle Atlantic states has more than doubled in the 20 years between 1929 and 1949 (Scattergood and McKown, 1951).

POPULATION CYCLES

Many reports have been interpreted as indicating regular and predictable periodicities in the abundance of certain species of insects and mammals, and supposed cycles have been reported for commercial fish catches. However, the evidence is not conclusive, since there is always the possibility of chance coincidence. Irregularity in the periods of fluctuations is certainly the general rule. Cole (1951) and others have shown that purely random variations in environmental conditions would be consistent mathematically with practically all numerical maxima and minima observed in vertebrate populations and with variations in tree-ring width. The evidence presented by Burkenroad (1946) concerning a 14-year periodicity in the abundance of starfish has been noted previously.

From an examination of temperature variations in surface water off New Brunswick, Canada from 1921 to 1947, Hachey and McLellan (1948) concluded that cycles of 3.3, 9 and 15 years were involved, and they have indicated similar trends for other localities along the Atlantic coast. Four years of warmer water have alternated more or less regularly with similar periods of colder water, but the deviations have not been extensive and random fluctuation would seem to be a more plausible explanation.

Hutchinson (1950) concluded from a study of the guano deposits on the Peruvian coast that a well marked 7-year cycle in the inshore movement of warm water and in associated biological catastrophes had occurred regularly from 1864 to 1939; he found no evidence of such a cycle prior to 1864. He concluded therefore that this rhythm is nonpersistent, as are so many meteorological cycles. The deposits on one of the islands showed no trace of this periodicity.

If it should be proved that there are predictable long-term periodic cycles in meteorological conditions or in the physical and chemical phenomena of the environment, then it might be expected that populations of plants and animals would fluctuate accordingly (Allee, *et al.*, 1949; Dice, 1952), but thus far the available information on population abundance seems to indicate that nearly all of the fluctuations have occurred at irregular intervals and have resulted from irregular changes in one or more of the environmental conditions.

A full discussion of this subject may be found in "Symposium on cycles in animal populations" (Hewitt, 1954).

SUMMARY AND CONCLUSIONS

The foregoing examples of fluctuations in populations of marine invertebrates indicate that annual changes of considerable magnitude are of general occurrence. Some of these are evidently due to concurrent changes in environmental conditions (including chemical and physical alterations of the water), to enemies, to disease, and to changes in substrate and in ocean currents. Others are due to migration or introduction to new localities.

Records of local populations of dinoflagellates, starfish, oysters, clams and mussels over long periods show that maximum and minimum populations have sometimes followed each other immediately but that populations of medium size are more numerous than those with either extreme.

Maximum and minimum populations generally occur at irregular and unpredictable intervals with no satisfactory indication of long-term periodic or rhythmical cycles; it is concluded that the supposed periodicities are the result of random variations in the complex environmental conditions, including diseases.

The records show that the reproductive capacity of many marine invertebrates is such that relatively few individuals under favorable conditions can produce a maximum population in a single generation. Overpopulation has been frequent and has often been followed by a rapid decline in numbers, since the competition for space or food was too severe for survival.

Resurgent populations have sometimes resulted from the arrival of vast numbers of pelagic larvae transported from localities several miles distant by ocean currents. Except in bays and partially confined bodies of water, there is little chance that a large proportion of the larvae will settle in the immediate vicinity of their place of origin.

Introduction of a species to a new locality has sometimes resulted temporarily in a high rate of multiplication and territorial expansion, usually followed by a rapid decline in numbers. More frequently the introduced species has found the new locality unsuitable for reproduction and has been rapidly eliminated.

The populations of most commercially important species, with the exception of lobsters, have declined more rapidly during the past decade than at any earlier period of similar length.

Useful as well as harmful species, when introduced intentionally or accidentally, have sometimes become permanent members of the local fauna.

On the Pacific coast an inverse correlation was found between the mean annual temperature of the water and the growth rate of mussels, as well as the populations of dinoflagellates.

Catastrophic changes in the populations have been observed occasionally or at irregular intervals. These have resulted from excessive heat or cold, heavy rains and floods, heavy surf, adverse ocean currents, loss of associated vegetation, industrial wastes, excessive abundance of dinoflagellates, or epidemics of parasitic diseases, with the destruction of many or nearly all individuals of susceptible species over large areas.

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